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Interaction between insect strain and artificial diet in diamondback moth development and reproduction

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Abstract

The economical production of physiologically and behaviorally competent diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is critical to most research and control programs against this insect. Although a few laboratory-adapted colonies are currently maintained on artificial diets, the establishment and adaptation of feral DBM onto semi-synthetic diets is often difficult. Understanding the interactions between insect strain and diet may be critical to the process of laboratory adaptation as well as to the successful use of laboratory-reared insects in the field. As such, the objective of this study was to investigate the interaction between several DBM colonies/strains and different natural and semi-synthetic diets. Specifically, we examined the effect of different diets on the length of development, percent survival, adult weight, female fecundity, and adult longevity for two feral and one laboratory-adapted strain of DBM. Significant interactions were observed between diet and laboratory-adapted and feral strains, and also between diet and different feral strains with respect to many of the growth and development parameters tested. Therefore, the performance of one strain of DBM on a particular diet was not necessarily predicted by the performance of another DBM strain on the same diet. However, the soy-based diet developed and reported herein performed well for all three DBM strains tested. In future efforts to colonize feral DBM, we suggest that researchers assay different diet formulations in order to identify a semi-synthetic diet that is most suitable for the particular DBM strain under consideration.

Introduction

The economical production of physiologically and behaviorally competent diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) is critical to most research and control programs against this insect (Shelton et al., 1991). Both augmentative biological control and autocidal genetic control of DBM require an efficient mass-rearing system. Although a few laboratory-adapted colonies exist in the United States and Europe there has been a fair amount of difficulty establishing colonies of DBM on artificial diets. As a consequence, researchers have often opted for rearing DBM on live plants even though this practice requires more labor, additional space, and greatly increases the chance for microbial contamination. Colonies of DBM are currently being maintained on mustard seedlings in the United States (G.L. Leibee, pers. comm.), cabbage leaves in Mauritius (Carpenter, pers. obs.), sawi leaves in Malaysia (Omar & Mansor, 1993), rapeseed seedlings (Koshihara & Yamada, 1976) and radish seedlings in Japan (Shirai, 2000), and on *Tropaeolum majus*, a wild host of DBM, in Vietnam (Nguyen Thi & Nguyen Than, 2001).

Only limited published information currently exists on rearing DBM on semi-synthetic diets. Biever & Boldt (1971) used a modified semi-synthetic diet originally developed by Berger (1963) for *Heliothis* spp. to rear DBM. They reported that DBM percent survival on this diet was 70.00%. Hsiao & Hou (1978) reported that only 58.83% of the DBM larvae reached

Table 1. Diets used in the *Plutella xylostella* diet suitability study. Amounts are sufficient to prepare 500 ml[a]

Ingredients	B&B[b]	H&H[b]	Wheat-G	Wheat-G/Y	Soy-B	Pinto-B	Pinto-B/C
Wheat germ (g)	15.00	15.00	23.10	15.00	–	22.00	22.00
Casein (g)	17.50	17.50	17.50	17.50	17.50	–	–
Pinto bean meal (g)	–	–	–	–	–	47.00	47.00
Soy flour (g)	–	–	–	–	15.00	–	–
Cabbage flour (g)	6.25	15.00	15.00	15.00	15.00	–	15.00
Brewers' yeast (g)	–	–	–	8.10	8.10	–	–
Torula yeast (g)	–	–	–	–	–	14.10	14.10
Sucrose (g)	17.50	17.50	17.50	17.50	17.50	–	–
Vitamin premix (g)	5.00	5.00	5.00	5.00	5.00	–	–
Ascorbic acid (g)	2.00	2.00	2.00	2.00	2.00	1.45	1.45
I-Inositol (g)	–	0.09	0.10	0.10	0.10	–	–
Choline chloride (g)	0.50	0.50	0.50	0.50	0.50	–	–
Wesson salts (g)	5.00	5.00	5.00	5.00	5.00	–	–
Aureomycin (g)	0.75	0.50	0.50	0.50	0.50	–	–
Sorbic acid (g)	–	–	1.00	1.00	1.00	0.44	0.44
Methyl-P (g)	0.75	0.75	1.00	1.00	1.00	0.88	0.88
Formaldehyde (37%) (ml)	0.25	0.25	–	–	–	0.34	0.34
Cholesterol (g)	–	1.25	1.25	1.25	1.25	–	–
Oil (ml)	–	3.50	3.50	3.50	3.50	–	–
(type)		(linseed)	(soy)	(soy)	(soy)		
KOH solution (ml)	2.50	2.50	2.50	2.50	2.50	–	–
Alphacel (g)	2.50	2.50	2.50	2.50	2.50	–	–
Agar (g)	11.25	11.25	11.25	11.25	11.25	5.60	5.60
Water (ml)	420	420	420	420	420	323	323

[a]Bio-Serv® DBM diet recipe is proprietary.
[b]as published in J.H. Hsiao & R.P. Hou, 1978.

pupation when using the Biever & Boldt diet and that roughly 1/3 of the adults emerging from these pupae had deformed wings. Hsiao & Hou (1978) further modified the Biever and Boldt diet and reported that percent survival during continuous rearing varied between 45.73–58.30%. Agui et al. (1975) formulated diets to rear *Mamestra brassicae* in Japan that could be used to rear DBM. Percent survival for DBM on these diets was between 35.00 and 39.13%. Shelton et al. (1991) compared the developmental and reproductive rates of a single population of DBM reared on artificial diet and rape seedlings and the influences of each rearing method on DBM used in insecticide and host-plant-resistance trials. Percent survival was quite variable, with values ranging from 4.40–54.20% on artificial diet versus 24.00–56.50% on rape seedlings. The authors nonetheless concluded that rearing DBM on artificial diet is more efficient and cost effective than rearing DBM on rape seedlings.

Research on other pest lepidopterans suggests that understanding the interactions between insect strain and diet may be critical to the process of laboratory adaptation as well as to the successful use of laboratory-reared insects in the field (Carpenter & Wiseman, 1999). As such, the objective of our study was to investigate the interaction between several DBM colonies/strains and different natural and semi-synthetic diets. Specifically, we examined the effect of different diets on the length of development, percent survival, adult weight, female fecundity, and adult longevity for two strains of DBM maintained on host plants and one laboratory-adapted strain of DBM maintained on meridic diet.

Table 2. Quantitative analysis of protein and fat content of the different diets used in the *Plutella xylostella* diet suitability studies

Diet	% Protein	% Fat
B&B[a]	29.41	0.93
H&H[a]	25.38	3.35
Wheat-G	23.81	5.04
Wheat-G/Y	26.62	4.17
Soy-B	27.43	5.79
Pinto-B	26.04	2.90
Pinto-B/C	24.43	2.78
Bio-Serv®[b]	20.64	2.42
Cabbage	12.76	1.35

[a]as published in J.H. Hsiao & R.P. Hou, 1978.
[b]Bio-Serv® DBM diet recipe is proprietary.

Materials and methods

Test insects. Three different colonies/strains of DBM were used in our studies, two from the Southeastern United States (Tifton, GA and Apopka, FL) and one from the island of Mauritius, situated in the Indian Ocean off the east coast of Africa. The Tifton laboratory-adapted colony was initiated from field-collected material from cabbage (*Brassica oleracea* var. *capitata*) in North Florida in 1993, and had been in continuous culture at the USDA-ARS Crop Protection and Management Research Unit in Tifton, GA for 103 generations when this study was initiated. No wild DBM have been introduced in this culture since its establishment. The Tifton colony is maintained on a pinto bean-based artificial diet similar to the one described in Burton (1969) for lepidopterans of the family Noctuidae. The Apopka colony is maintained at the University of Florida Mid-Florida Research and Education Center in Apopka, FL. This colony was established in 1998 from DBM collected in the field from collard (*Brassica oleracea* var. *acephala*) near Sanford, FL and had been in continuous culture for approximately 32 generations at the initiation of our experiments. The Apopka colony is housed in a large 'free-flight' rearing room and reared on planted trays of mustard seedlings (*Brassica juncea*). The DBM colony in the island of Mauritius was established in 1998 from field-collected DBM from cabbage and is maintained in greenhouse cages (approximate size is $75 \times 50 \times 50$ cm) on cabbage plants and excised leaves of cabbage. Field-collected DBM are introduced into the greenhouse cages several times each month, however, no controlled matings between introduced and colony DBM are performed. Approximately 25 generations had been reared in the greenhouse at the time the experiments were initiated. Because the Tifton colony has been maintained on an artificial diet and has been in culture for many more generations than the other two colonies, the Tifton colony is referred to as the 'laboratory-adapted' strain and the Apopka and Mauritius colonies are referred to as 'feral' strains.

Eggs from the Tifton DBM strain were collected on rectangles of creased aluminum foil (7.6×15.2 cm) dipped in cabbage juice that hung inside a screen cage ($30.5 \times 30.5 \times 30.5$ cm) containing newly emerged (<24 h) DBM adults. The moths were allowed to mate and lay eggs for 48 h at 21 °C, 50% r. h., and L12:D12. Aluminum foil sheets with eggs from the DBM strain in Apopka were sent to the USDA-ARS laboratory in Tifton to be used in these experiments. In Mauritius, newly emerged greenhouse adults were collected and placed inside a plexiglass cage ($60 \times 30 \times 30$ cm) and allowed to mate and lay eggs on paper towel rectangles (5×4 cm) dipped in cabbage juice (27 ± 2 °C, ambient r.h., and L12:D12) for 48 h. All experiments on the Tifton and Apopka strains were conducted at the USDA-ARS laboratory in Tifton and the Mauritius strain was assayed in Mauritius at the Agricultural Research and Extension Unit (AREU) laboratories in Reduit.

Artificial diets. Eight diets were prepared for these experiments: Bio-Serv® Premix (BIO) for DBM, Biever & Boldt diet (B&B) (as published in Hsiao & Hou, 1978), and Hsiao & Hou diet (H&H) (Hsiao & Hou, 1978). In B&B and H&H the required amount of vitamin B solution was substituted for 5 g of USDA vitamin premix available from Bio-Serv®. Other diets used included a wheat germ-cabbage flour-based diet (Wheat-G) developed by the authors, the Wheat-G diet with the addition of brewers' yeast (Wheat-G/Y), a soybean and cabbage flour-based diet (Soy-B) developed by the authors, the modified pinto bean-based diet (Pinto-B) used in Tifton to rear DBM, and the pinto bean-based diet with the addition of 15 g of cabbage flour (Pinto-B/C). The ingredients and amounts to prepare 500 ml of each diet are listed in Table 1 except for the Bio-Serv® diet which is proprietary. The diets were mixed and poured into plastic containers (either $25.4 \times 25.4 \times 7.6$ cm or 16 ounce round) and allowed to cool. The surface of the diets was scarified using a wire comb and the Pinto-B and Pinto-B/C diets were toasted in a small oven for 5 min to remove sur-

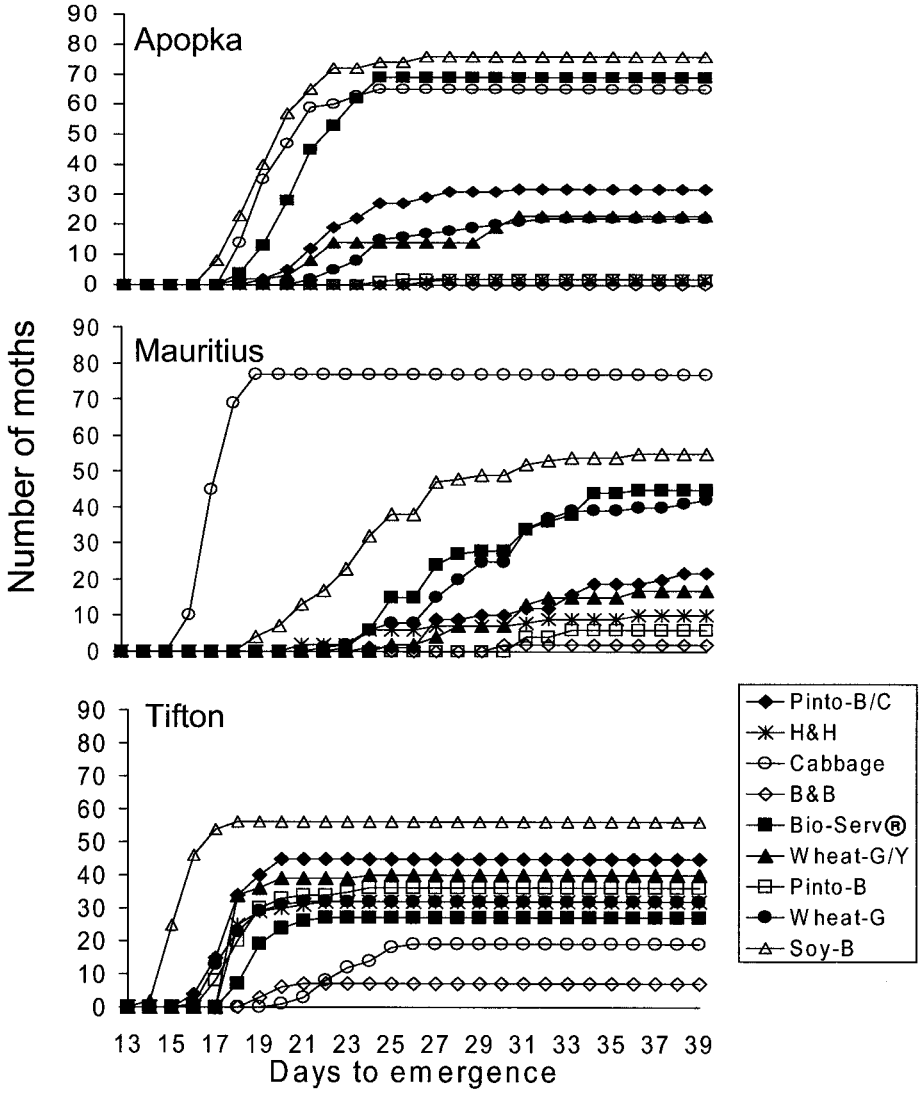

Figure 1. Developmental time, rate of adult emergence, and number of adults produced when Tifton, Apopka, and Mauritius strains of *Plutella xylostella* were reared on different diets.

face moisture that might drown neonate DBM. Fresh cabbage leaves were used as a control.

All diets, including cabbage, were analyzed to determine their protein and fat content. The amount (%) of nitrogen present was determined using a FP-228 Nitrogen Determinator (Model 601-700, Leco, St. Joseph, MI), and protein content was estimated using the formula 6.25× % nitrogen (Helrich, 1990). Fat content (%) was determined using the ether extraction technique and a Labconco-Goldfisch Fat Extractor (Labconco Corporation, Kansas City, MO). Results of the analysis are shown in Table 2.

Diet suitability experiments – effect on adult emergence and weight. Diets were cut into 2 × 2 × 1 cm sections and dispensed into 1 ounce clear Solo® plastic cups. In order to prevent moisture build-up in the cups a 1.5 cm circular opening was cut into the lids and replaced by a circle of filter paper. Newly emerged (<6 h-old) neonates were collected (as they hung from their silk threads) and placed on the diet with a fine tipped brush. Ten neonates per cup and ten replicates per DBM strain were set-up. Cups were kept in chamber at 22 °C, 35% r. h., and L00:D24 and checked every 48 h. New diet cubes or cabbage leaves were added as needed. After date of first pupa-

Table 3. Interaction of insect strain and diet on the percentage survival (±SD) of three different strains of *Plutella xylostella* (n = 100)

Diet[a]	Insect strain[b]		
	Apopka	Mauritius	Tifton
Pinto-B	2.00 ± 6.32 B b	6.00 ± 8.43 C b	36.00 ± 17.76 A a
Pinto-B/C	32.00 ± 20.44 B a	20.00 ± 12.47 BC a	45.00 ± 11.79 A a
B&B	0.00 ± 0.00 B a	2.00 ± 6.32 C a	7.00 ± 13.37 B a
Bio-Serv®	69.00 ± 24.69 A a	45.00 ± 19.00 B ab	27.00 ± 18.29 B b
Cabbage	65.00 ± 15.09 A a	77.00 ± 17.03 A a	19.00 ± 11.97 B b
Wheat-G	20.00 ± 20.00 B a	46.00 ± 20.11 B a	32.00 ± 23.48 A a
Wheat-G/Y	23.00 ± 14.94 B a	17.00 ± 13.37 C a	40.00 ± 16.33 A a
H&H	2.00 ± 4.22 B b	10.00 ± 14.14 C ab	32.00 ± 19.32 A a
Soy-B	76.00 ± 19.55 A a	55.00 ± 12.69 A a	56.00 ± 22.71 A a

[a]Numbers within a column followed by the same uppercase letter are not significantly different ($P \leq 0.05$, Tukey-Kramer; SAS Institute, 1989).
[b]Numbers within a row followed by the same lowercase letter are not significantly different ($P \leq 0.05$, Tukey-Kramer; SAS Institute, 1989).

Table 4. Interaction of insect strain and diet on the mean (±SD) developmental time (in days) for three different strains of *Plutella xylostella*

Diet[a]	Insect Strain[b]		
	Apopka	Mauritius	Tifton
Pinto-B	–	31.80 ± 1.10 A a	18.61 ± 1.57 B b
Pinto-B/C	22.63 ± 2.50 A b	30.10 ± 3.58 A a	17.93 ± 1.10 B c
B&B	–	–	19.71 ± 0.76 AB
Bio-Serv®	21.03 ± 1.69 AB b	28.51 ± 3.81 A a	19.19 ± 1.06 B b
Cabbage	19.73 ± 1.52 B b	17.39 ± 0.85 C c	23.05 ± 1.65 A a
Wheat-G	24.59 ± 2.81 A b	28.30 ± 3.17 A a	18.61 ± 1.50 B c
Wheat-G/Y	24.43 ± 4.64 A b	30.00 ± 3.22 A a	18.35 ± 1.08 B c
H&H	26.50 ± 0.71 A a	26.50 ± 5.23 AB a	18.41 ± 0.95 B b
Soy-B	20.50 ± 2.71 AB b	24.50 ± 3.82 B a	17.18 ± 1.13 B c

[a]Numbers within a column followed by the same uppercase letter are not significantly different ($P \leq 0.05$, Tukey-Kramer; SAS Institute, 1989).
[b]Numbers within a row followed by the same lowercase letter are not significantly different ($P \leq 0.05$, Tukey-Kramer; SAS Institute, 1989).

tion was recorded, cups were checked daily for adult emergence. Date of first adult emergence was recorded as were the number of pupae obtained per cup per treatment. Emerging adults were collected, sexed, and weighed after they excreted the meconium.

Diet suitability experiments – effect on DBM adult fecundity and longevity. The Tifton DBM strain was assayed on the following diets: Bio-Serv®, Soy-B, Pinto-B, Pinto-B/C, and cabbage was used as a control. The Apopka strain was assayed on Bio-Serv®, Soy-B, Pinto-B, Pinto-B/C, and cabbage. The Mauritius strain was assayed on Soy-B and cabbage. All assays were conducted in 16 oz. Solo® plastic containers containing the appropriate diet. Small (1.25 × 2.5 cm) aluminum foil egg sheets with DBM eggs were incubated for 48 h at 23.8 °C, ambient r.h., and L12:D12 and hung inside the diet cups. In this way, emerging larvae spun down directly on the diet. Cups were kept at 22 °C, 35% r. h., and L00:D24 and checked every 48 h. Once formed, DBM cocoons were removed and placed individually into small (1 ounce) plastic cups. Date of adult emergence was recorded and adults were sexed, weighed after excreting the meconium, and individually paired with adults emerging from the same diet treatment in small plastic cups. Ten pairs per diet treatment were used. Pairs were provided with a 10% carbohydrate solution on a cotton

wick. Moths were allowed to mate and lay eggs for 24 h and were transferred to new plastic cups every 24 h until female death. The number of eggs laid per female per day was recorded. Female and male adult longevity was noted. Plastic cups with eggs from days one and two, were incubated for 48 h (23.8 °C, ambient r.h., and L12:D12) and egg hatch was assessed as an indication of whether the females had mated. Only mated females were used in the analysis.

Data analysis. Data were analyzed by PROC-GLM (SAS Institute, 1989) as a three factor ANOVA. Factors for analysis included diet, insect strain, insect gender, and all interactions. Dependant variables were percent survival, developmental time, adult weight, fecundity, and longevity. When significant differences were indicated, means were separated by the Tukey-Kramer statistic at $P = 0.05$ (SAS Institute, 1989). The relationship between the amount of fat or protein in the diet and the life history parameters of each DBM strain was explored using PROC-CORR (SAS Institute, 1989). The rate of increase for each DBM strain on different diets was calculated using a modification of the formula by Birch (1948) ($r = \log_e R_0 / T$). For our purposes, R_0 = mean number of female progeny reaching adulthood from each female parent, and T = the sum of the mean developmental time (neonate-adult) plus the mean number of days for females to lay 50% of their eggs.

Results

There was a significant interaction between insect strain and diet on the percentage survival of DBM ($F = 12.45$; $df = 16, 243$; $P < 0.0001$) (Table 3). Survival for the Apopka strain was significantly higher when larvae were fed Soy-B, Bio-Serv®, and cabbage than when larvae fed on other diets. The Mauritius DBM strain had significantly higher survival on cabbage and Soy-B than on the other diets tested. Survival for the laboratory-adapted Tifton strain was significantly higher when insects were fed Soy-B, Pinto-B/C, Pinto-B, Wheat-G, Wheat-G/Y, and H&H diets than when fed on other diets. Survival for each DBM strain was lowest when larvae were fed the B&B diet. Comparing all artificial diets, the highest percentage survival for each strain was observed when larvae were reared on the Soy-B diet. The interaction between diet and insect strain for percentage survival of DBM was greatest when larvae were reared on Pinto-B, Bio-Serv®, cabbage, and H&H diets. Our results on the B&B diet are in sharp contrast to previously published figures on percent survival (58.83–70.00%) for DBM (see Introduction). In our experiments almost no feral DBM survived to adulthood (0.00% for Apopka and 2.00% for Mauritius) when fed on the B&B diet.

Data on cumulative emergence for each DBM strain on different diets are shown in Figure 1. A significant interaction between developmental time (neonate-adult) and DBM strain was observed when the DBM were fed different diets ($F = 55.31$; $df = 13, 706$; $P < 0.0001$) (Table 4). Mean developmental time for the Apopka strain (Figure 1a) was shortest when larvae were fed cabbage and longest when larvae were fed H&H diet. The developmental times for the Apopka DBM fed on Soy-B and Bio-Serv® diets were not significantly different from that recorded for larvae that were fed cabbage. The Mauritius strain (Figure 1b) also developed significantly faster on cabbage than on the other diets. However, the mean developmental time for the Tifton strain (Figure 1c) was shortest when larvae were fed the Soy-B diet. Comparing all artificial diets, the most rapid development in all strains tested occurred when larvae were reared on the Soy-B diet.

There was a significant three-way interaction between insect strain, insect gender, and diet with respect to adult weights ($F = 3.85$; $df = 13, 706$; $P < 0.0001$) (Figure 2). In general, the DBM strain from Apopka produced the lightest adults. Diet type did not significantly affect the weights of male or female Apopka moths, however, mean weights were greatest when larvae were fed Soy-B diet. The highest female weights for the Mauritius DBM strain were obtained when larvae were fed cabbage. These weights were significantly higher than the mean weights of the Mauritius DBM females reared on Pinto-B, Wheat-G/Y, and Pinto-B/C diets. The type of diet did not significantly affect male weights for the Mauritius DBM. Conversely, the mean weight of the Tifton DBM females was lowest when larvae were fed cabbage. All artificial diets except B&B produced significantly heavier females for the Tifton strain than did cabbage. Although the mean weights for Tifton DBM males followed a similar pattern as female weights across diets, diet type did not significantly affect the weight of the Tifton males.

Data on cumulative oviposition for cohorts of DBM females from the different strains fed on different diets are presented in Figure 3. Apopka females (Figure 3a) reared on the Soy-B and Pinto-B/C diets

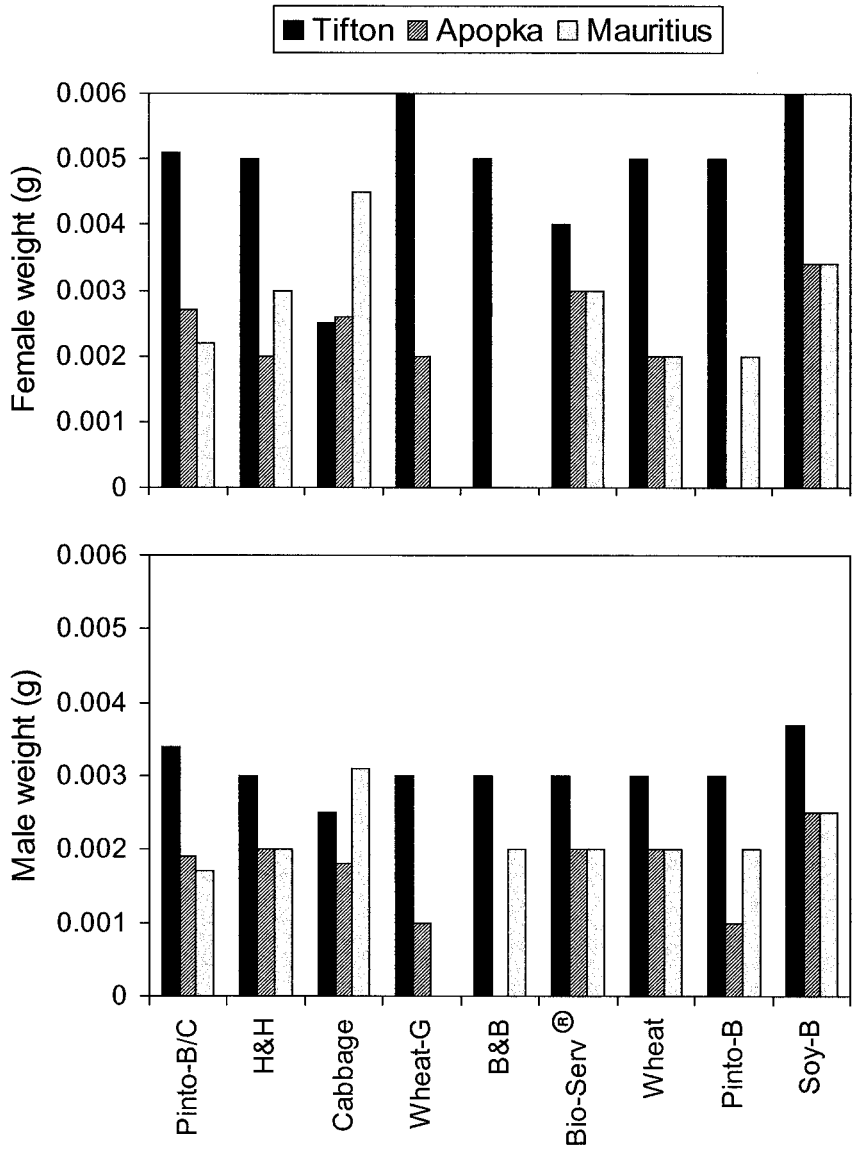

Figure 2. Male and female adult weights when Tifton, Apopka, and Mauritius strains of *Plutella xylostella* were reared on different diets.

laid significantly more eggs than females from other diets. There was no significant difference in the mean number of eggs laid by Mauritius females (Figure 3b) reared on cabbage and Soy-B. Significantly more eggs were laid by females from the Tifton strain (Figure 3c) developing from the Pinto-B and Pinto-B/C diets as compared to those from other diets. Tifton females that developed from cabbage laid significantly fewer eggs than females that developed from all other diets except Wheat-G and Bio-Serv® (B&B and H&H diets were not included in the fecundity test because of poor survival). A significant interaction was observed between the mean number of eggs laid by DBM females from different strains when all diets were included in the analysis ($F = 12.70$; $df = 5, 306$; $P < 0.0001$). We also observed a significant interaction between diet and strain when only the diets from which Mauritius females developed (cabbage and Soy-B) were included in the analysis ($F = 4.96$; $df = 2, 124$; $P < 0.0085$) (Table 5). No significant difference in fecundity was observed between DBM strains in females fed on cabbage. However, the Apopka and Tifton females laid significantly more eggs than Mauritius females when reared on Soy-B (Figure 3).

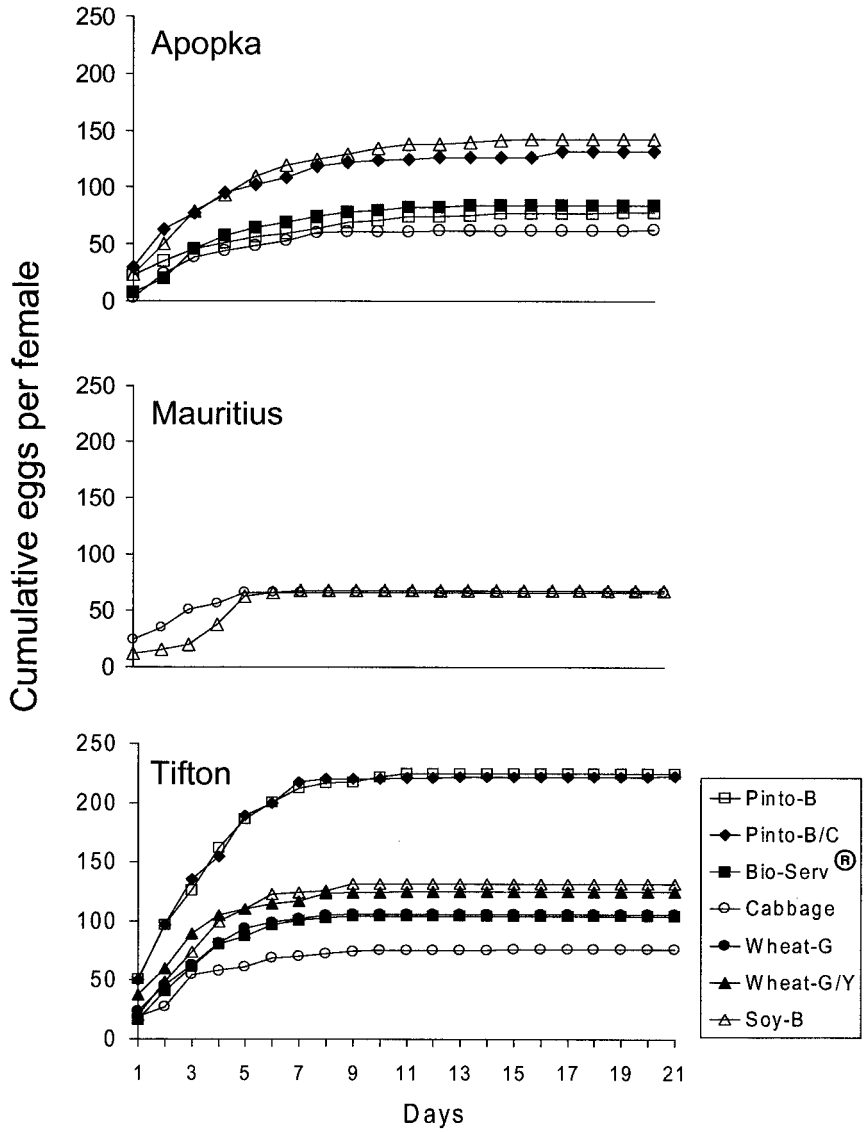

Figure 3. Cumulative mean number of eggs and rates of oviposition for females when Tifton, Apopka, and Mauritius strains of *Plutella xylostella* were reared on different diets.

Table 5. Interaction of insect strain and diet on the mean fecundity (±SD) of three different strains of *Plutella xylostella* (n = 100)

Diet[a]	Insect strain[b]		
	Apopka	Mauritius	Tifton
Cabbage	60.23 ± 24.98 B a	66.11 ± 33.20 A a	75.55 ± 33.33 B a
Soy-B	141.57 ± 46.49 A a	67.83 ± 12.05 A b	131.37 ± 93.71 A a

[a]Numbers within a column followed by the same uppercase letter are not significantly different ($P \leq 0.05$, Tukey-Kramer; SAS Institute, 1989).
[b]Numbers within a row followed by the same lowercase letter are not significantly different ($P \leq 0.05$, Tukey-Kramer; SAS Institute, 1989).

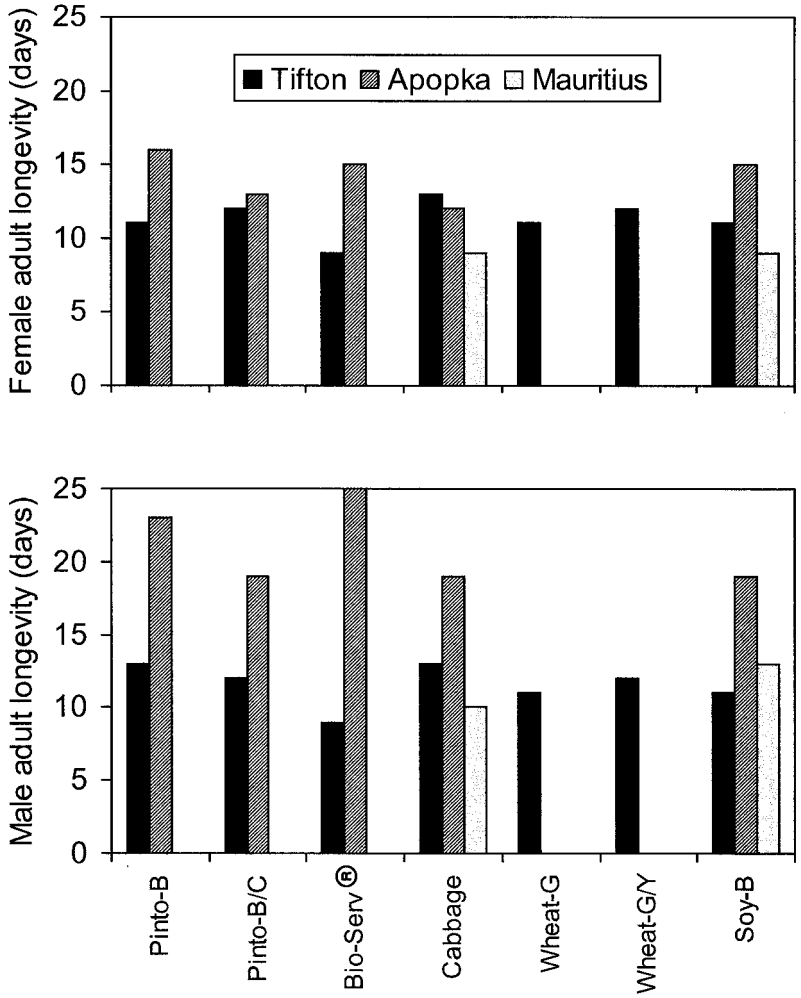

Figure 4. Male and female adult longevity when Tifton, Apopka, and Mauritius strains of *Plutella xylostella* were reared on different diets.

Data on adult longevity for DBM males and females from different strains reared on different diets are shown in Figure 4. In general, DBM males lived longer (mean = 16.02 days) than did females (mean = 12.22 days), and the DBM from Apopka was the longest-lived strain (17.6 days vs. 12.02 days for Tifton & 10.02 days for Mauritius). However, adult longevity was significantly affected by an interaction between insect strain and gender ($F = 7.46$; $df = 2, 306$; $P < 0.0007$) and between insect strain and diet ($F = 4.79$; $df = 5, 306$; $P < 0.0003$). When reared on artificial diets, Apopka DBM males and females were longer lived than males and females from the other two strains. However, Tifton females lived longer than females from the other two strains when reared on cabbage.

The rate of increase (r) for each DBM strain reared on the different diets is presented in Figure 5. The Tifton strain had the highest rate of increase when reared on the Pinto-B, Pinto-B/C, and Soy-B diets and the lowest rate of increase when fed on cabbage. The highest rate of increase for Apopka DBM was when insects were fed on Soy-B diet. When reared on Bio-Serv®, cabbage, and Soy-B diets, the rate of increase for the Apopka strain was greater than the rate of increase for the Tifton strain. The highest rate of increase when DBM were fed on cabbage was obtained for the Mauritius strain. This strain also exhibited a moderate rate of increase when reared on the Soy-B diet.

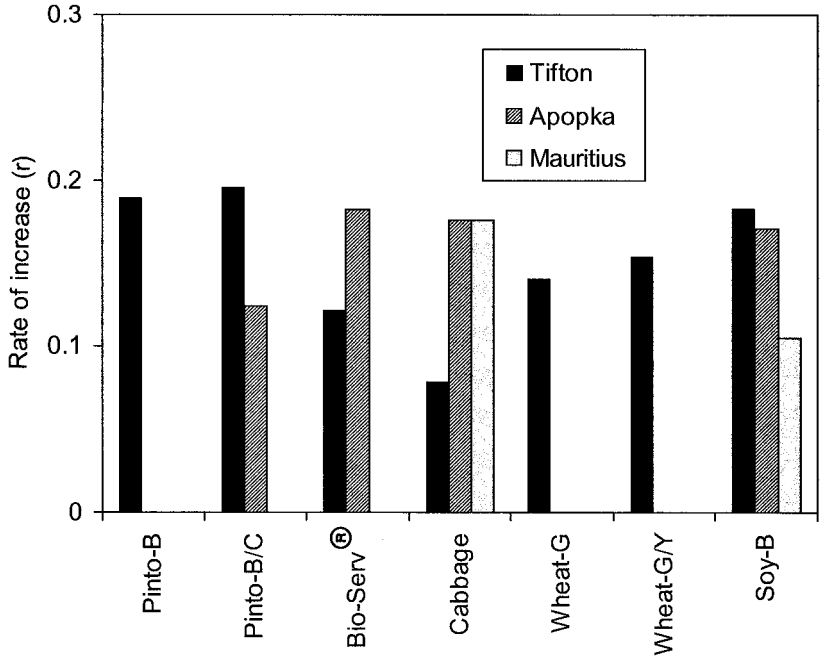

Figure 5. Rate of increase (r) when Tifton, Apopka, and Mauritius strains of *Plutella xylostella* were reared on different diets ($r = \log_e R_0 / T$; where R_0 is the mean number of female progeny reaching adulthood from each female parent, and T is the sum of the mean developmental time (neonate - adult) plus the mean number of days for females to lay 50% of their eggs (modified from Birch, 1948).

Discussion

Several studies have demonstrated that insect strain and degree of laboratory adaptation can influence the ability of an insect to develop on different diets, including its natural host plant. Quisenberry & Whitford (1988) and Whitford et al. (1992) evaluated colonies of *Spodoptera frugiperda* (J.E. Smith) representing two host strains (corn & rice) on different artificial diets. They found that both strains responded to the diets differently as a result of the type of meridic diet on which they were maintained for the previous 11 generations. Slansky & Wheeler (1992) compared the performance of larvae of *Anticarsia gemmatalis* (Hübner) from a laboratory colony in existence for >100 generations with that of feral (field-strain) larvae. They found that field-strain larvae exhibited prolonged development and a lower biomass-relative growth rate when fed an artificial diet compared with the laboratory-strain larvae. Conversely, laboratory-strain larvae grew more slowly than field-strain larvae when both were fed foliage of a natural host plant. These authors suggest that the poor performance of the laboratory-strain on the host plant may be due to a reduced ability to detoxify a plant foliage allelochemical(s), which may have a deleterious effect on the conversion of absorbed food to biomass. Similar results have been reported from studies of other lepidopteran species (Carpenter & Wiseman, 1999; Kumar, 1993; Thomas & Boethel, 1993; Wiseman & Carpenter, 1995; Yu, 1986, 1988).

In general, the laboratory-adapted Tifton DBM performed better on most artificial diets when compared to the feral strains (Apopka & Mauritius). Similar to many laboratory-adapted colonies of other lepidopteran species, this strain performed quite poorly on its natural host plant, cabbage (see Carpenter & Wiseman, 1999). The developmental time for the Tifton DBM was significantly longer on cabbage than on any of the artificial diets except for the results obtained for larvae fed on B&B diet. In fact, the B&B diet consistently gave the poorest results for all DBM stains in all the parameters we measured. Conversely, both feral DBM strains (Apopka & Mauritius) performed well on cabbage but results for these strains varied when they were reared on different semi-synthetic diets. Overall, the Soy-B diet, developed during the initial phase of this study, was the most suitable diet as it supported adequate biotic potential for each of the three strains of DBM we examined.

The concentration of nutrients in an artificial diet may have an effect on the growth rate of insects. Wise-

man & Carpenter (1995) reported that an increased amount of protein in an artificial diet fed to *Helicoverpa zea* (Boddie) produced heavier pupae and reduced the amount of time required to develop from a neonate to a pupa. However, in the present study we found no correlation between the amount of protein or fat in the different diets (Table 2) and the DBM life history parameters measured. The type of protein or the type of sugars associated with the ingredients providing the protein source might be more important in making diets better suited for rearing particular DBM strains than the amount of protein (within the range of our study).

It is difficult to ascertain why the published diets for DBM, namely B&B and H&H, gave such poor results especially when used to rear feral strains (Figure 1a & b). The small amount of cabbage flour contained in B&B diet (6.25 g per 500 ml) may have affected the feeding rate of DBM larvae. Furthermore, the B&B diet does not contain *i*-inositol, which is reported to be a phagostimulant (Hsiao & Hou, 1978) or cholesterol, which is essential for successful insect molting and wing formation (Chapman, 1971). H&H was the only diet that called for raw linseed oil and both B&B and H&H diets do not contain sorbic acid. Linseed oil can quickly turn rancid and become toxic to insects and sorbic acid prevents mold contamination. In fact, one of the biggest problems with both of these diets in our study was mold contamination of the medium.

A determination of the causal mechanisms associated with the interaction between DBM strain and insect diet is beyond the scope of the present study. However, we suggest two possible explanations for past difficulties in colonizing feral DBM on artificial diets. First, the only published diets for DBM, namely B&B and H&H, have often been used in initial colonization attempts for this insect. Our experimental results showed that both diets resulted in very low performance compared to the other diets tested (Figure 1) and were more susceptible to mold contamination. This was especially true when feral strains (Apopka [Figure 1a] & Mauritius [Figure 1b]) were reared on these diets. Second, the interaction between diet and DBM strain has not been fully considered in the past. In our studies, this interaction was observed between laboratory-adapted (Tifton) and feral strains (Apopka & Mauritius) and also between different feral strains. Therefore, the performance of one strain of DBM on a particular diet does not necessarily predict the performance of another DBM strain on the same diet. Nonetheless, all three DBM strains performed well on the soy-based diet developed in our study. In future efforts to colonize feral DBM in the laboratory, we suggest that researchers assay different diet formulations in order to identify a diet that is most suitable for the particular DBM strain under consideration.

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